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RECENT STUDIES ON CERTAIN SPECIES OF *RICCIA**

ALEXANDER W. EVANS

The genus *Riccia*, as ordinarily understood, includes the two subgenera *Euriccia* and *Ricciella*. In typical *Euriccia* the air chambers are very narrow and clearly extend in a single layer from the compact ventral tissue of the thallus to the upper surface; in typical *Ricciella* the chambers are much broader and seem to be arranged in two or more layers when cross sections of the thallus are examined. Largely on the basis of these differences *Ricciella* has sometimes been considered a distinct genus. In all probability, however, its broad chambers are really in a single layer, and the superimposed arrangement which they seem to show is due to the obliquity of their course. This being the case the distinction in the chambers become reduced to a difference in width, and even this distinction has been proved inconstant as a differential character. Juel (5) has shown, for example, that *R. Bischoffii* Hüb., a widely distributed species of the Old World has narrow chambers in the median portion of the thallus and broad chambers toward the margin; and Von Gaisberg (4, p. 264) has made similar observations in the case of *R. Gougetiana* var. *armatissima* Lev., a Mediterranean form. The latter author cites in addition certain species of *Ricciella* in which some of the air spaces are almost as narrow as those of typical *Euriccia*. In view of these transitional forms connecting *Euriccia* and *Ricciella*, it seems wisest to follow the usual custom and consider the groups subdivisions of a single genus.

Until a few years ago *Riccia fluitans* L. was universally regarded as a clearly defined species of *Ricciella* with a wide geographical distribution. It was said to occur in two distinct states or forms: an aquatic form without rhizoids, which never produced sexual organs and sporophytes; and a terrestrial form with rhizoids, which produced sporophytes with some degree of frequency. The fertile terrestrial form was said to develop when the aquatic form was deposited on the mud, upon the evaporation of the surrounding water, while the aquatic form was said to develop when the terrestrial form was flooded. Most writers considered that the aquatic form, in spite of its sterility, represented the typical condition of the species, and the terrestrial form was often separated as the variety *canaliculata* (Hoffm.) Lindenb., in spite of the apparent ease with which one form could be converted into the other. *R. fluitans*, moreover, was regarded as the only member of the subgenus *Ricciella* that was able to live indefinitely

*Contribution from the Osborn Botanical Laboratory.

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as an aquatic, unattached plant. At the same time several closely related species that grow on soft mud along the borders of ponds or streams, but not in the water itself, have been described. Two such species, *R. Huebeneriana* Lindenb. and *R. pseudo-Frostii* Schiffn., appear in recent European manuals; in North America *R. Huebeneriana* has likewise been reported, but *R. pseudo-Frostii* is replaced by *R. Sullivantii* Aust. Another more distantly related species, *R. Frostii* Aust., may be mentioned in this connection; this grows in similar localities and has a wide distribution on both sides of the Atlantic.

Recently, especially in Europe, the opinion is becoming more and more widely held that some of these other species of *Ricciella* may live as aquatic plants too, giving rise to states or forms which resemble the aquatic form of "*R. fluitans*" in a marked degree. The advocates of this opinion hold that these various aquatic forms have been included in the old conception of "*R. fluitans*" and that the latter is, in consequence, not the aquatic form of a definite species but merely an aggregation of the aquatic forms of various distinct species.

One of the earliest papers bearing on these points was published by Torka (7) in 1906 and dealt with *R. Huebeneriana*, which he discovered near Schwiebus in eastern Germany, growing as a terrestrial plant on mud. He placed some of this mud, which bore rosettes of the *Riccia*, in a glass receptacle and flooded it with water. After a while the tips of the thalli began to elongate and fork, but instead of clinging to the mud these new growths failed to develop rhizoids and often became detached, floating freely on the surface of the water. Here they remained green for some time but eventually perished unless the water was drawn off. If this was done the floating fragments would be left on the mud and would renew their growth, giving rise to attached plants of a fairly normal appearance. The part that had previously floated, however, failed to develop rhizoids and assumed a brownish color, apparently indicating a disintegration of the tissues.

On the basis of these results Torka concluded that *R. Huebeneriana* would be able to maintain itself as an aquatic plant in the open, if the places where it grew were flooded. In his opinion floating plants of this character would be the only ones to survive the winter, attaching themselves to the substratum and developing normally after the water had sunk to its usual level in the spring. He thus ascribed to *R. Huebeneriana* an amphibious habit, comparable with that of *R. fluitans*.

Five years later (8. p. 205) he announced the discovery of aquatic plants of *R. Huebeneriana* near Nakel and Zablocie in Poland and described them as a new variety under the name *Ricciella Hübeneriana* var. *natans*. In his description he notes the lack of rhizoids and the tendency of large mats of thalli to break up into small mats as the older parts die. As a result of this process the surface of the water becomes closely covered with innumerable plants in the late summer and early autumn. At the edge of the water some of these floating fragments attach themselves to decaying plants or to the moist earth, where they develop rhizoids as they continue their growth showing a tendency to develop into a more robust terrestrial form, just as the floating fragments did in his culture experi-

ments. Torka does not state whether these plants produced sporophytes or not. In 1914 he distributed excellent specimens of his var. *natans* (9, No. 51) from the Zablocie locality. These present the appearance of a slender aquatic *R. fluitans*, as this species is usually understood.

It is unfortunate that Torka's evidence is not more conclusive. Although, in his cultures, the tips of the thalli often detached themselves and floated on the water, nothing is said about their growing while in this condition. It is implied, in fact, that the floating fragments carried on a very precarious existence unless they came in contact with some firm substratum. The mere fact that they remained green for a while would hardly show that they represented a true aquatic form of *R. Huebeneriana*. In order to prove that such a form had been produced it should have been shown that the plants in question were capable of continuing their growth and development in their new environment. With regard to the Polish specimens of his var. *natans* the evidence is lacking that these actually represent *R. Huebeneriana*. The only way in which this could be proved would be by means of morphological characters either in the thallus or in the spores. No such characters are given, and, although the attached plants are said to resemble the attached fragments of *R. Huebeneriana* in the water cultures, these fragments (as represented by Torka's figure) are hardly representative of *R. Huebeneriana* as it normally appears. The case is further weakened by the fact that he does not report the normal terrestrial *R. Huebeneriana* in the vicinity of the var. *natans*, although he cites a single station for it at a somewhat distant Polish locality.

In 1916 Donaghy (1) published a series of interesting field observations on *R. fluitans*, as it occurs in Indiana. He reports that the so-called terrestrial form is uncommon in his region but notes its occasional appearance "on mud flats and wet fields during the autumn." This form produces sporophytes in abundance. The aquatic form is abundant around Angola, Fort Wayne, and Terre Haute, where "during the summer and autumn mats . . . can be found floating in ponds and sluggish streams," sinking to the bottom in the winter and remaining there until spring. Although plants beneath the ice remain uninjured, those "frozen in the ice are much winter-killed, the apical ends alone remaining green." During "spring these plants make rapid growth, and by summer patches of thalli again dot the ponds and streams." When, owing to evaporation, the water becomes low, "mats of plants are" often "washed upon the wet edges of the ponds," and "in favored places the thalli coming in contact with the wet soil develop rhizoids . . . and open air-chambers." Whether such plants ever develop sexual organs and sporophytes remained uncertain, Donaghy's evidence on this point being wholly negative. He reports a case where plants "remained alive in wet shaded places . . . in contact with the earth sufficiently long to fruit," and yet "no sporophytes were formed."

In Donaghy's opinion these sterile terrestrial plants, derived from the aquatic plants, were distinct from the so-called terrestrial form of *R. fluitans*, and he failed to find the latter on the mud of ponds where the aquatic form was growing. He concludes from his observations that "it seems very doubtful

if the aquatic form ever changes into the terrestrial form or fruits" or "if the so-called terrestrial *R. fluitans* and the aquatic *R. fluitans* belong to the same species." Here again, it would be interesting to know just how the two terrestrial plants differed from each other, but no distinguishing morphological characters are given. It is stated, however, that the reticulate spores of the so-called terrestrial *R. fluitans* measure 75–90 μ in diameter, and this would seem to show that the material had been correctly determined and had not been confused with the closely related *R. Huebeneriana* or *R. Sullivantii*, the spores of which are smaller.

Although Donaghy's observations throw doubt on the present delimitation of *R. fluitans*, he evidently considers that the so-called aquatic form of the species is something definite. The contrary opinion is clearly expressed by Familler (3, p. 12), and he presents certain morphological distinctions to support his views. According to his statements it has now been definitely established that *Riccia fluitans* consists of at least two or three aquatic forms of various *Ricciae*. He therefore does not accept "*R. fluitans*" as a species but ascribes specific rank instead to what most writers regard as the fertile terrestrial form of *R. fluitans*. For this he takes up the old name *R. canaliculata* Hoffm. (as some of his predecessors have done) and calls the aquatic form of this species forma *fluitans* (L.) Fam. Under *R. Huebeneriana* he includes Torka's var. *natans*, as *Riccia Huebeneriana* forma *natans* (Torka) Fam., and he recognizes further an aquatic form of *R. pseudo-Frostii*. Since, however, he regards this species as a variety of *R. Huebeneriana* its aquatic form receives the name *Riccia Huebeneriana* var. *pseudo-Frostii* forma *natans* Fam. He implies that other species of *Riccia* may likewise have aquatic forms and suggests that a Mexican specimen, collected by W. Schaffner many years ago and determined by A. Braun as *Ricciella fluitans*, may be the aquatic state of *R. Frostii*, but he does not give this plant a formal name.

In separating the aquatic form of *R. canaliculata* from those of *R. Huebeneriana*, he assigns to the first very long air-spaces and to the second shorter and more crowded air spaces; in separating the aquatic form of the var. *pseudo-Frostii* from that of the ordinary *R. Huebeneriana*, he assigns to the first marginal air spaces about as long as wide and a clearly defined median band and to the second marginal air spaces about twice as long as wide and an indistinct median band. These differences are shown on *pl. 1* and *2*; the figures give the impression that the morphological distinctions between the various aquatic forms are based on variable characters and that careful culture studies would be necessary before the taxonomic value of these characters could be accurately estimated. Of course, if it could be proved that an aquatic form with long air spaces gave rise to typical *R. canaliculata* and that a form with short spaces gave rise to *R. Huebeneriana*, the differences in the air-spaces would at once assume a greater importance. Unfortunately proof of this character is lacking, and some of Von Gaisberg's culture experiments, to be mentioned below, have yielded contradictory results.

Von Gaisberg's studies on *Riccia* (4), carried on in Goebel's laboratory at Munich, throw an interesting light on some of the questions here discussed.

Evidence is first presented to show that an aquatic form of *Riccia* is not necessarily sterile, even in Europe. In old specimens collected by A. Braun at Tempelhof near Berlin and labeled by him *R. "fluitans fructifera"* archegonia are present in abundance. These specimens lack rhizoids and present every appearance of having been aquatic in habit. Wherever archegonia are situated the thallus is distinctly broader, and where the archegonia are separated from one another by sterile tracts the thallus shows a series of marginal lobes on each side, indicating the position of the archegonia. Von Gaisberg compares the Tempelhof *Riccia* with the African *R. Dinteri* Steph. (apparently a manuscript species), which was found on stones in a spring. Here too the position of the archegonia is marked by marginal lobes. Unfortunately he gives us no data regarding the spores in either case. It should be mentioned in this connection that Familler (2, p. 166) had already noted the occurrence of fruit in the aquatic form of "*R. fluitans*", before he had developed his later ideas regarding the species. His specimens came from Bavaria, but he tells us nothing about their structural features.

In his experimental work Von Gaisberg first utilized an aquatic form of "*R. fluitans*" growing in the university greenhouse at Munich. When this was transferred to soil it gave rise to what he called a "broad form," but even in this condition remained perfectly sterile, so that it was impossible to assign it to any known species on the basis of characters derived from the spores. He then turned his attention to an aquatic *Riccia* which he found in the vicinity of Starnberg in Bavaria. This plant was determined by Familler, presumably on the basis of its morphological features, as *R. Huebeneriana*; but when it was cultivated on soil it gave rise to a "broad form" essentially like that derived from the greenhouse material. Von Gaisberg expresses the opinion that this "broad form" is distinct from "*R. fluitans* f. *canaliculata*" and also from *R. Huebeneriana*. Although he thus differs from Familler, so far as the latter's determination of the Starnberg material is concerned, he agrees with him in considering "*R. fluitans*" a composite species and cites, in further defense of this view, the wide variation in width exhibited by herbarium specimens bearing this name.

In the brief description of the "broad form" it is noted that the air chambers are more or less polygonal; in cross section the thallus is bounded on each side by a single large chamber but elsewhere the chambers appear to be in two layers or sometimes, in the median portion, in three. Although these features might serve to distinguish the plant from *R. Huebeneriana*, as this species is usually described, they would hardly distinguish it from the "*forma canaliculata*": and it is unfortunate that no other differential characters are indicated.

The work here reviewed shows that our knowledge concerning "*R. fluitans*" and certain terrestrial forms or species of the subgenus *Ricciella* is still far from complete. It shows further that additional culture experiments and accurate morphological comparisons will be necessary before satisfactory conclusions can be reached. The species of this subgenus are exceedingly variable and react to slight environmental differences. *R. Huebeneriana*, for example, although seemingly very distinct from *R. pseudo-Frostii* in size, in color and in the shape

of the cross section of the thallus, is not so in reality. Familler (3, p. 14) has shown that typical *R. pseudo-Frostii*, in some of his cultures, became directly transformed into *R. Huebeneriana*, and Nicholson (6, p. 202) has confirmed these results by careful observations in the field. There is every reason to suppose that *R. fluitans* is fully as variable as *R. Huebeneriana*. The so-called "broad form" of Von Gaisberg and the terrestrial form obtained by Donaghy in his study of the aquatic *R. fluitans* should therefore be subjected to a more rigid scrutiny than they have yet received, in order to determine whether their distinctive features are constant or inconstant in character. Until this is done their status must remain uncertain. Renewed search should likewise be made for the aquatic form of *R. fluitans* in fruiting condition, in order to determine whether or not the marginal lobing of the Tempelhof specimens represents a constant feature and also to compare the spores with those of the terrestrial form.

YALE UNIVERSITY

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THE MOSSES OF THE OXFORD UNIVERSITY EXPEDITION TO
SPITZBERGEN, 1921¹

H. N. DIXON, M. A., F. L. S.

The mosses sent to me for determination were collected by three of the botanists who took part in the expedition, in June—August, 1921. Part of them were collected and sent to me by Mr. John Walton, and were collected about Klaas Billen Bay, mostly in the neighborhood of Bruce City. The remainder were sent by Mr. V. S. Summerhayes and were mostly collected by himself in various localities (Bear Id., Prince Charles Foreland, &c.); but a certain number of them were gathered by Mr. C. S. Elton in the neighborhood of Klaas Billen Bay.

The number of species found among these collections was about 82, out

¹ Constituting Number 17 of the Results of the Oxford University Expedition to Spitzbergen, 1921.